

References and Notes

1. R. W. Sperry, M. S. Gazzaniga, J. E. Bogen, in *Handbook of Clinical Neurology*, P. J. Vinken and G. W. Bruyn, Eds. (North-Holland, Amsterdam, 1969), vol. 4, p. 273.
2. M. S. Gazzaniga, *The Bisected Brain* (Appleton-Century-Crofts, New York, 1970).
3. D. Galin, *Ann. N.Y. Acad. Sci.* **299**, 397 (1977).
4. P. Flechsig, *Lancet* **1901-II**, 1027 (1901); W. Hewitt, *J. Anat.* **96**, 355 (1962); N. Geschwind, *Brain* **88**, 237 (1965); P. Yakovlev and A. Lecours, in *Regional Development of the Brain in Early Life*, A. Minkowski, Ed. (Blackwell, Oxford, 1967), p. 3; A. Lecours, in *Foundations of Language Development*, E. H. Lenneberg and E. Lenneberg, Eds. (Academic Press, New York, 1975), vol. 1, p. 121.
5. O. Selnes, *Brain Lang.* **1**, 111 (1974).
6. A. Salamy, *Science* **200**, 1409 (1978).
7. S. Kumar, G. M. Bogen, J. E. Bogen, *Proc. Soc. Neurosci.* **3**, 69 (1977).
8. We were not explicitly investigating possible sex differences in this study. We tested only girls to avoid confounding with possible sex factors and because results of pilot studies indicated that 3-year-old girls may tolerate the test procedures better than boys.
9. The "same"-"not-same" concept was introduced visually with a set of wooden blocks. Difference was marked by high contrast in color and number (one red versus four blue). When labeling became reliable, contrast was first reduced, then the child was switched to visual-plus-tactile discrimination of the fabrics, and finally to tactile discrimination alone. Criteria for admission to each succeeding step of pretesting were specified, and perseveration was guarded against. Of 20 3-year-olds available for testing, five were rejected from the sample, two for unreliable same-different judgments with blocks and three who could not generalize the judgments to the easiest pillows. Two 5-year-olds were rejected for unreliable tactile judgments. The 3-year-olds were briefly rescreened at the start of each session. We found this rescreening to be a useful indication of the child's attentiveness on that particular day. It was frequently necessary to stop testing the youngest children because they were too easily distracted and to continue the next day.
10. Five of the 3-year-olds were allowed to palpate the pillows briefly between the thumb and fingers rather than having the pillow rubbed over the fingers by the experimenter. The results were identical.
11. As an alternative statistical strategy, we also considered a repeated measures analysis of variance to compare uncrossed versus crossed errors (within-subject factor) as a function of age (between-subjects factor). However, we judged the *t*-test on crossed errors as percentages of total errors to be a more appropriate analysis both because it takes into account each child's total error rate and because it is the most direct test of our major hypothesis. The *t*-test was calculated on log transforms of percentage scores because logarithms are symmetrically distributed about 0. To completely analyze other factors in the data, two three-factor analyses of variance were computed, one for uncrossed errors and one for crossed errors. The two types of errors were analyzed separately because they involve different factors—hand stimulated for uncrossed, and direction of crossing for crossed errors. Uncrossed errors were analyzed in an age (3- versus 5-year-olds) by hand (right versus left) by trial type (same versus not same) repeated measures analysis of variance. Trial type was the only significant factor, showing more N-S errors ($P < .001$). This factor also interacted with age: the 5-year-olds made more N-S errors than the 3-year-olds ($P = .011$). These differences did not affect the crossed-uncrossed error difference between age groups. The age factor was not significant for uncrossed errors ($P = .064$). Crossed errors were analyzed in an age (3- versus 5-year-old) by direction (crossing from right to left hand versus left to right hand) by trial type (same versus not same) repeated measures analysis of variance. The 3-year-olds showed more crossed errors than the 5-year-olds ($P < .001$). This result is parallel to that of the *t*-test but does not have the benefit of correction for total error rate. There was also a main effect of direction, crossing from right to left producing more errors than from left to right ($P = .046$). The interpretation of this effect is not clear. Again, as with uncrossed errors, there was a main effect of trial type, showing more N-S than S errors ($P = .038$), although trial type did not interact with age in the crossed errors analysis. A significant triple interaction ($P = .018$) also appeared because the 5-year-olds tended to make more errors on N-S than S trials crossing in both directions, whereas the 3-year-olds made more S errors on right-to-left trials and more N-S errors on left-to-right trials. These more detailed analyses of trial type, hand stimulated, and direction of crossing do not elucidate the age dependence of crossed versus uncrossed error rate, which was similar for S and N-S errors as well as for crossing right to left and left to right.
12. J. E. Bogen, *Bull. Los Angeles Neurol. Soc.* **34**, 73 (1969); *ibid.*, p. 135.
13. ——— and G. M. Bogen, *ibid.* **34**, 191 (1969).
14. S. Orton, *Reading, Writing, and Speech Problems in Children* (Norton, New York, 1937); S. F. Witelson, *Science* **195**, 309 (1977).
15. D. Galin, *Arch. Gen. Psychiatry* **31**, 572 (1974); ———, R. Diamond, D. Braff, *Am. J. Gen. Psychiatry* **134**, 578 (1977); J. G. Beaumont and S. J. Dimond, *Br. J. Psychiatry* **123**, 661 (1973).
16. We acknowledge the contributions of R. Diamond who began the development of this experiment and P. Lund and S. May who helped collect the data. We also thank California Assemblyman John Vasconcellos. This work was supported by NIH biomedical research support grant 5S07 RR0575505. D.G. was supported in part by NIMH career award MH28457. We also thank the children, teachers, and school administrators for patience and cooperation.

3 November 1978

Search Image Formation in the Blue Jay (*Cyanocitta cristata*)

Abstract. *Blue jays trained to detect Catocala moths in slides were exposed to two types of slide series containing these moths: series of one species and series of two species intermixed. In one-species series, detection ability increased with successive encounters with one prey type. No similar effect occurred in two-species series. These results are a direct demonstration of a specific search image.*

Predators guided by vision often prey differentially on different prey types (1), a response frequently taken as evidence for a predator's use of a specific search image (2, 3). This evidence has included a number of different behavioral patterns, such as a predator's choosing one prey type more frequently than would be expected from the prey's relative density (1), a predator's responding to a familiar

prey type before responding to a newly introduced type (2), or a predator's delaying before responding to a novel, cryptic prey type (3). However, as Dawkins (4) and Krebs (5) have pointed out, the search-image concept should be used only when the predator's ability to detect prey improves as a function of recent encounters with the prey type. Much of the existing evidence for search image can

be explained by prey preferences, by differences in palatability, ease of capture, or handling time among the prey types, or avoidance of an unfamiliar food object (4). We present data showing direct effects of search image upon the detection of prey.

We studied blue jays searching for cryptic *Catocala* moths (Noctuidae), which are normally preyed upon by jays in the wild (6). We trained jays to respond differentially to the presence or absence of *Catocala* moths in projected images (7). To test for search image in these experienced birds, we controlled the sequence of images they encountered. The jays were exposed to a succession of slides of one prey type; their detection of the moths in this series was compared with that when the slide series contained two prey species intermixed (8). The search image hypothesis predicts that the jays should be increasingly able to detect the moths with successive encounters with one cryptic prey type, but should not show rapid changes in detection when searching for two species in a series of slides.

Five blue jays, obtained in the Amherst, Massachusetts, area when 10 to 12 days old and hand raised in the laboratory, were subjects. All birds had been trained to detect *Catocala* moths in projected images (7) and were familiar with the species used in this study. The birds were maintained at 80 percent of their free-feeding weight throughout the experiment. The apparatus was a pigeon chamber (Lehigh Valley Electronics). A food magazine was located centrally on the intelligence panel, with an 11.4- by 7.5-cm stimulus key mounted to the left of the magazine and a round advance key 2.54 cm in diameter mounted to the right. Slides were projected onto the stimulus key by a programmable projector (Kodak Carousel) mounted behind the panel. Reinforcement was half a *Tenebrio* larva delivered into the magazine by a feeder (Davis Universal) mounted on top of the chamber.

Positive slides contained the image of a moth and negative slides contained no moth. Each trial began with the illumination of the advance key with red light. When the advance key was pecked once, an image was projected onto the stimulus key. If the projected slide was positive, ten pecks at the stimulus key (correct response) resulted in reinforcement. Reinforcement was followed by a 10-second intertrial interval (ITI) to allow ingestion of the reward before the next trial began. A peck at the advance key on positive trials (incorrect response) produced a 60-

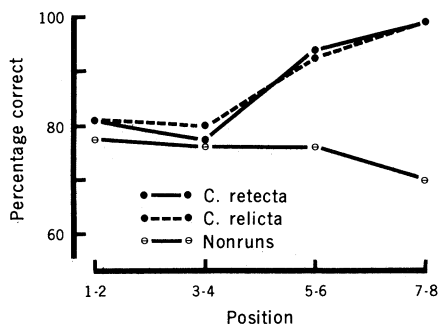


Fig. 1. Mean percentage correct responses on positive (moth) slides within runs (*C. resecta* and *C. relictata*) and nonruns as a function of the position of each slide in the test series (first through eighth positive slide).

second ITI. On negative trials, the tenth peck at the stimulus key (incorrect response) was followed by a 60-second ITI, but one peck at the advance key (correct response) produced a 4-second ITI.

A detailed description of the slides has been reported (7). For this study, two species of *Catocala* were used in the test slides: *C. relictata* (white forewings with prominent stripes of black and gray, which usually rests head up on white birch); and *C. resecta* (gray forewings with a prominent disruptive pattern of brown lines, which usually rests head down on dark bark such as oak). These moths appeared only in cryptic conditions on their species-typical substrate (7, 9).

Search image formation was tested by embedding one of three types of 16-slide series within a discrimination session: "run," eight positive and eight matched negative slides, all positives containing *C. relictata*, or all positives containing *C. resecta*; or "nonrun," four positive slides of *C. relictata* and four positive slides of *C. resecta*, intermixed with eight matched negative slides. Thus, in a run, the jays searched for one species of moth, and in a nonrun, they searched for two species.

The jays were exposed to these slides in sessions of 24 trials, two sessions a day (with 1.5 hours between sessions) for 12 days. Each session included the 16 slides in the test series (run or nonrun) and eight other slides (four positive of a third species, *C. cara*, four negative) randomly chosen from our collection. The test series of 16 slides began equally often on trials 3, 4, or 5 of the session in order to make the start of the test series less predictable. The jays were exposed to a total of eight sessions containing a run of *C. resecta*, eight sessions containing a run of *C. relictata*, and eight sessions containing nonruns.

The positions of the eight positive slides within the test series were designated positions 1 through 8. The effects of the position of the slide on detection were examined by analyzing percentage correct responses with analysis of variance. The percentage correct increased across position in both run (*C. relictata* and *C. resecta*) conditions, but not across position in nonruns (Fig. 1). The interdependent effects of test series type and position of the slides on performance resulted in a significant interaction of these factors ($P < .005$). There was also a significant main effect of test series type (run or nonrun) on performance ($P < .025$). The jays responded at a mean of 87.8 percent correct on *C. resecta* runs, at 88.1 percent correct on *C. relictata* runs, and at 75.0 percent correct on nonruns.

The percentage correct increased across position of the negative slides within the run conditions, but not within the nonrun condition (Fig. 2). The differential effects of test series type on performance on negative slides resulted in a significant interaction of these factors ($P < .025$). In addition, there was a main effect of test series type upon percentage correct on negative slides ($P < .005$). The jays responded at a mean of 87.7 percent correct on negative slides within *C. resecta* runs, at 84.9 percent correct within *C. relictata* runs, and at 76.6 percent correct within nonruns (10).

These data provide, to our knowledge, the first direct evidence for search image as an improvement in the predator's ability to detect a particular prey type as a result of recent successive encounters with that prey type. Our procedures held all variables constant except the sequence in which prey types were encountered. Thus the changes in the performance of the jays can be explained only in terms of changes in detection, as the search-image hypothesis requires (4, 5).

These results also show that a predator is better able to detect the absence of a prey type when search image is used. This effect can be observed only with procedures that require a recordable response to the absence of prey. However, this phenomenon is probably of considerable importance, since it would allow a predator to quickly leave an area devoid of prey, and this response can be an important component of efficient foraging (11). It is possible that search image involves not only changes in the detection of a particular prey type, but also changes in the efficiency with which the predator locates and scans an appropri-

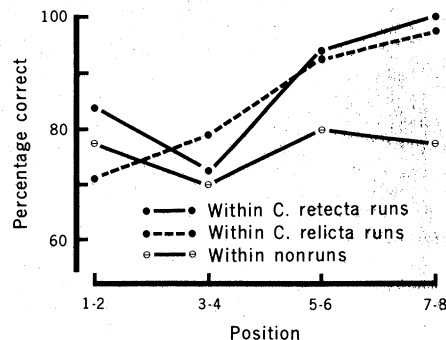


Fig. 2. Mean percentage correct responses on negative (no moth) slides within each condition, as a function of the position of each slide in the test series (first through eighth negative slide).

ate substrate. This possibility is supported by our results.

Our results support the hypothesis that the visually guided predator experiences short-term changes in its ability to detect cryptic prey, and these changes are determined by what the predator has most recently detected. Such a mechanism would undoubtedly contribute to sudden intense predation on one particular species, a response commonly observed in the wild (1). Additional research is needed to investigate these perceptual changes with varying densities of available prey types.

ALEXANDRA T. PIETREWICZ*

ALAN C. KAMIL

Department of Psychology, University of Massachusetts, Amherst 01003

References and Notes

1. L. Tinbergen, *Arch. Neerl. Zool.* **13**, 265 (1960); J. H. Mook, L. J. Mook, H. S. Heikens, *ibid.*, p. 448; D. M. Ware, *J. Fish. Res. Bd. Can.* **28**, 1847 (1971); H. C. Mueller, *Nature (London)* **233**, 345 (1971); M. D. Rausher, *Science* **200**, 1071 (1978).
2. H. J. Croze, *Z. Tierpsychol. Beih.* **5** (1970); J. Alcock, *Behaviour* **46**, 174 (1973); J. A. Allen and B. Clarke, *Nature (London)* **220**, 501 (1968).
3. L. de Ruiter, *Behaviour* **4**, 222 (1952).
4. M. Dawkins, *Anim. Behav.* **19**, 566 (1971).
5. J. B. Krebs, in *Perspectives in Ethology*, P. P. G. Bateson and P. H. Klopfer, Eds. (Plenum, New York, 1973), pp. 73-111.
6. T. D. Sargent, *J. Lepid. Soc.* **27**, 175 (1973).
7. A. T. Pietrewicz and A. C. Kamil, *Science* **195**, 580 (1977).
8. These birds were experienced only with the intermixed sessions.
9. Slides were prepared in matched pairs, identical except for the presence or absence of a moth, by pinning a dead moth into position on a tree, taking a picture of the scene, then removing the moth and taking another picture.
10. Although the data here are grouped for all birds, these same effects of condition and position of the slides in the test series were reflected in the performance of the individual birds.
11. E. L. Charnov, thesis, University of Washington (1973); G. Thomas, *Anim. Behav.* **22**, 941 (1974).
12. This research is part of a thesis submitted to the University of Massachusetts by A.T.P. We thank T. D. Sargent for his advice and for supplying the moths, and M. A. Novak and J. W. Donahoe for their constructive suggestions and comments. Supported in part by NSF grants GB-30501 and BNS-76-80275.

* Present address: Department of Psychology, Emory University, Atlanta, Ga. 30322.

6 October 1978; revised 20 March 1979